Vision Research 51 (2011) 1075–1085

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Relative contributions of the two eyes to perceived egocentric visual direction in normal binocular vision

Deepika Sridhar [a,*], Harold E. Bedell [a,b]

[a] College of Optometry, University of Houston, 505 J Armistead Bldg, Houston, TX 77204-2020, USA
[b] Center for NeuroEngineering & Cognitive Science, University of Houston, Houston, TX 77204-4005, USA

ARTICLE INFO

Article history:
Received 17 December 2010
Received in revised form 21 February 2011
Available online 1 March 2011

Keywords:
Egocentric visual direction
Oculocentric visual direction
Pointing
Vergence
Disparity
Hering's laws of visual direction

ABSTRACT

Perceived egocentric direction (EVD) is based on the sensed position of the eyes in the orbit and the oculocentric visual direction (eye-centered, OVD). Previous reports indicate that in some subjects *eye-position* information from the two eyes contributes unequally to the perceived EVD. Findings from other studies indicate that the *retinal* information from the two eyes may not always contribute equally to perceived OVD. The goal of this study was to assess whether these two sources of information covary similarly within the same individuals. Open-loop pointing responses to an isolated target presented randomly at several horizontal locations were collected from 13 subjects during different magnitudes of asymmetric vergence to estimate the contribution of the position information from each eye to perceived EVD. For the same subjects, the direction at which a horizontally or vertically disparate target with different interocular contrast or luminance ratios appeared aligned with a non-disparate target estimated the relative contribution of each eye's retinal information. The results show that the eye-position and retinal information vary similarly in most subjects, which is consistent with a modified version of Hering's law of visual direction.

1. Introduction

Perceived egocentric visual direction (EVD, the direction referenced to one's self, and specifically the head) is based on the combination of eye position and retinal information (oculocentric visual direction, OVD). Extraretinal signals of eye position provided by ocular muscle proprioception (Bridgeman & Stark, 1991; Buisseret & Maffei, 1977; Gauthier, Nommay, & Vercher, 1990; Steinbach & Smith, 1981) and efference copies (Bock & Kommerell, 1986; Bridgeman, 1995; von Holst & Mittelstaedt, 1950; Walls, 1951) allow the brain to monitor the position of the eyes in the orbits. OVD is the direction of an image with respect to a reference location on the retina (generally the fovea) or to one or more other retinal images (Howard, 1982; Mansfield & Legge, 1996; Walls, 1962). The perception of OVD is assumed to be mediated by a local sign mechanism (Charnwood, 1965; Hering, 1868/1977; Mather, 1969/1983; Matin, Pearce, Matin, & Kibler, 1966; Ogle, 1972; Ono & Mapp, 1995; Walls, 1951). According to this mechanism, each point in the visual cortex is associated with a specific retinal point and, for a specific eye position, each retinal point in turn is associated with a specific direction in space. Hering's laws of visual direction provide predictions for the combination of eye-position and retinal information to perceived EVD. According to these laws, the eye-position information from both eyes is averaged, and the perceived EVD of a foveated target lies on a line that passes from approximately midway between the eyes through the intersection of the visual axes (Barbeito & Ono, 1979; Hering, 1868/1977; Ogle, 1972; Ono, 1991; Ono & Weber, 1981; Verhoeff, 1925). Similarly, the retinal information from the two eyes is averaged to determine the perceived OVD of an object that is imaged at *similar* locations in the two eyes (Hering, 1868/1977; Nakamizo, Shimono, Kondo, & Ono, 1994; Sheedy & Fry, 1979; Verhoeff, 1925; Wheatstone, 1838).

There is general agreement among previous studies that the eye-position information from both eyes contributes to perceived EVD (Barbeito & Simpson, 1991; Erkelens, 2000; Ono & Weber, 1981; Park & Shebilske, 1991; Simpson, 1992). However, the results of these studies show that, during binocular viewing, some observers exhibit between-eye differences in the contribution of the eye-position information to perceived EVD. For example, Barbeito and Simpson (1991) measured the contribution of eye-position information from the two eyes during asymmetric vergence produced by stepping a target in front of only one eye, and reported that the eye-position information from each eye does not always contribute equally to the perceived EVD. Other studies showed either qualitatively (Charnwood, 1949) or quantitatively

* Corresponding author. Fax: +1 713 743 2053.
E-mail addresses: DSridhar.2010@alumni.opt.uh.edu (D. Sridhar), HBedell@Optometry.uh.edu (H.E. Bedell).

0042-6989/$ - see front matter © 2011 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2011.02.023

(Ding & Sperling, 2006, 2007; Francis & Harwood, 1951; Mansfield & Legge, 1996; Sheedy & Fry, 1979) that the *retinal* information from the two eyes contributes to perceived OVD. The results of these studies indicate that when the images in the two eyes differ in terms of luminance (Charnwood, 1949; Francis & Harwood, 1951; Verhoeff, 1933), contrast (Ding & Sperling, 2006, 2007; Mansfield & Legge, 1996), or blur (Charnwood, 1949), then the perceived OVD shifts towards the image with the higher luminance or contrast, or lesser blur, implying a differential weighting of the retinal information from the two eyes.

Although these previous studies evaluated the contributions of each eye's position or retinal information to perceived EVD and OVD, none of them addressed whether the two sources of information covary with respect to one another. An assumption that is made implicitly in the literature is that the position and the retinal information from each eye vary similarly. The purpose of the current set of experiments is to evaluate this implicit assumption. To do so, we determined in a group of normal observers the relative contributions to perceived direction of the eye-position and retinal information from the two eyes. We then compared these two measures within subjects to determine whether these two sources of information covary with one another.

2. General methods and subjects

Experiments 1 and 2 reported below in Sections 3 and 4 determined the contributions of eye-position and retinal information from the two eyes to perceived EVD and OVD, respectively. Relative contributions of *eye-position* information from the two eyes were determined from open-loop pointing errors. Relative contributions of the *retinal* information to perceived OVD were assessed by determining the perceived direction of images with binocular retinal image disparity compared to an image with no retinal image disparity. Experiments 2a and 2b determined the perceived OVD for *horizontally* disparate targets that differed either in contrast or luminance in the two eyes, respectively. Experiment 2c determined perceived OVD for *vertically* disparate targets that differed in contrast in the two eyes. Estimates of ocular dominance obtained by a hole-in-the-card test, comparison of monocular contrast sensitivities, and a blur-suppression test are reported in Section 5. Finally, in Section 6, we compare the relative contribution of eye-position and retinal information for the same subjects. Thirteen subjects participated in Experiments 1 and 2a. Twelve and ten subjects participated in Experiments 2b and 2c, respectively. All of the subjects had best-corrected visual acuity of at least 20/20 in each eye and were orthotropic. One subject had refractive errors of −4.50 D and −2.00 D in the right and left eyes, respectively. Except for this subject with anisometropia, none of the subjects had any history of abnormal binocular vision. The subjects wore their refractive correction during the experiments. All subjects voluntarily provided written informed consent in accordance with the tenets of the Declaration of Helsinki, after the University of Houston Committee for the Protection of Human Subjects had reviewed the experimental protocol.

The stimuli for all experiments were displayed on a 120-Hz frame-rate, gamma-corrected Clinton monochrome monoray monitor and viewed from a distance of 50 cm. The images presented to the two eyes were interleaved in alternate video frames. Subjects viewed the stimuli through FE-1 ferro-electric goggles (Cambridge Research Systems) that were attached to a stand with a chinrest. This set-up helped to minimize the subjects' head movements. Synchronization of the video frames of the monitor with the ferro-electric goggles allowed for dichoptic image presentation. Control observations confirmed that none of the images presented to one eye were visible to the contralateral eye.

3. Experiment 1: determination of the relative contribution of eye-position information to perceived EVD

3.1. Stimuli and methods

In Experiment 1, the relative contribution of eye-position information from the two eyes was determined using an open-loop pointing task. The pointing target was a 'cross' with a luminance of 2.5 cd/m^2 presented on the monitor with a black background, in a completely dark room. The horizontal and vertical bars of the cross had a length and width of 39.7 and 5.3 arc min, respectively. Pointing responses were collected with no vergence demand and for four magnitudes of asymmetric vergence demand (5 PD[1] divergence, 5, 10, and 15 PD convergence), all determined with respect to the plane of the display monitor. On each trial, the pointing target was presented at one of 15 horizontal locations with respect to the eye without the asymmetric vergence demand, and was displaced from this position by an amount equivalent to the magnitude of the required vergence demand for the eye with the vergence demand. The 15 locations were the center of the monitor, and seven locations spaced one PD apart to the right and left of the center.

After the subject fused the pointing target, (s)he indicated by pressing a button on a CT3 button box (Cambridge Research Systems) that (s)he was ready to point to the target. The shutters of the goggles then closed in front of both eyes, and a dim scale, marked horizontally in one PD intervals, replaced the pointing target on the screen. The scale was visible only to the experimenter. The subject pointed at the remembered location of the target using the index finger of the preferred hand, and the experimenter read the pointing response to the nearest half prism diopter. This sequence continued for 150 trials. The eye that responded to the asymmetric vergence demand and the magnitude of the vergence demand was randomized from trial to trial. After the subject removed his or her hand from the screen, a white screen was presented for 3 s before the next pointing target, to facilitate the visual recalibration of sensed eye position (Blouin, Amade, Vercher, Teasdale, & Gauthier, 2002). Because the pointing target was presented at a constant distance, the accommodative demand was kept constant throughout the experiment.

To ensure that the vergence response was equal to the vergence demand, horizontal fixation disparity was measured for each magnitude of vergence demand using a pair of dichoptic Nonius lines separated vertically by 1.75° while the subject fixated on the fixation cross. Fixation disparity was measured just before the trials on which the pointing target for the eye without the asymmetric vergence demand appeared at the center of the monitor and at 6 PD to the right and left.

For each of the 13 subjects, pointing errors were calculated as the difference between the location where the subject pointed and the location of the target on the monitor for the eye without the vergence demand. The pointing error was calculated for each target location and for each magnitude of asymmetric vergence demand for the two eyes. To account for idiosyncratic errors, the pointing errors obtained during binocular viewing without any vergence demand were averaged across the 15 pointing-target locations for each subject. These errors are referred to as constant errors. The "corrected" pointing error on each trial for each subject, including the trials without any vergence demand, was determined by subtracting the constant error from each pointing error. Correction for the constant errors facilitates the combination of data across days.

To evaluate whether the pointing *errors* vary systematically for the 15 locations of the pointing target on the screen, we fit regres-

[1] PD = prism diopter.

sion lines to each subject's data for the largest vergence demand (15 PD), separately for asymmetric demands presented to the left and the right eye. Of the 26 fitted regression lines, only four had a significant ($p < 0.05$) variation of the corrected pointing error with target location. Because the number of significant relationships is small despite no correction for multiple statistical comparisons, we concluded that the subjects' pointing errors do not exhibit any systematic dependence on the location of the target on the screen. Therefore, in subsequent analyses pointing errors were pooled across 15 target locations for each asymmetric vergence demand that were presented to the right and left eye.

Because the magnitude of the vergence response (as determined from the fixation disparity measurements) was approximately equal to the magnitude of the vergence demand for all magnitudes of vergence demand in all the subjects, 'corrected' pointing errors were plotted directly against the magnitude of asymmetric vergence demand, separately for asymmetric vergence of the right and the left eye, for each of the 13 subjects. A straight line was fit to the data (combined across sessions) by minimizing the squared errors between the data and the fitted line, separately for the corrected pointing errors obtained during asymmetric vergence of the right and the left eye. A *t*-test for equality of slopes was performed separately for the data of each subject to determine whether the absolute values of the slopes fit to the pointing errors for each eye differed significantly.

3.2. Results

Across all subjects and vergence demands, the average standard deviation of the pointing errors was 3.1 PD. The representative plots in Fig. 1 shows that the 'corrected' pointing errors are in the direction of the eye that makes the asymmetric vergence movement. Specifically, asymmetric convergence of the right eye produces pointing errors towards the left, whereas asymmetric convergence of the left eye results in pointing errors towards the right. Asymmetric divergence with each eye produces the opposite direction of pointing errors. In all of the subjects, the corrected pointing errors increase as the magnitude of the vergence demand increases. The expected slope of the best-fit line based on Hering's law of visual direction is +0.5 for asymmetric vergence of the left eye and −0.5 for asymmetric vergence of the right eye. Table 1 lists the slopes of the lines fit to the pointing errors during asymmetric vergence of each eye, and the ratio of the slopes (Right eye slope/Left eye slope) for each of the 13 subjects. As indicated at the bottom of the Table, the straight lines fit to the corrected pointing errors of the two subjects who performed the experiment twice had slopes that did not differ statistically between the two testing occasions. The slopes of the pointing-error functions determined for the left and right eyes differ significantly ($p \leqslant 0.05$) in six of the 13 subjects. The mean sum of the unsigned slopes in the 13 subjects was 0.99 ± 0.18, which is close to the value of 1 that is expected on the basis of Hering's law.

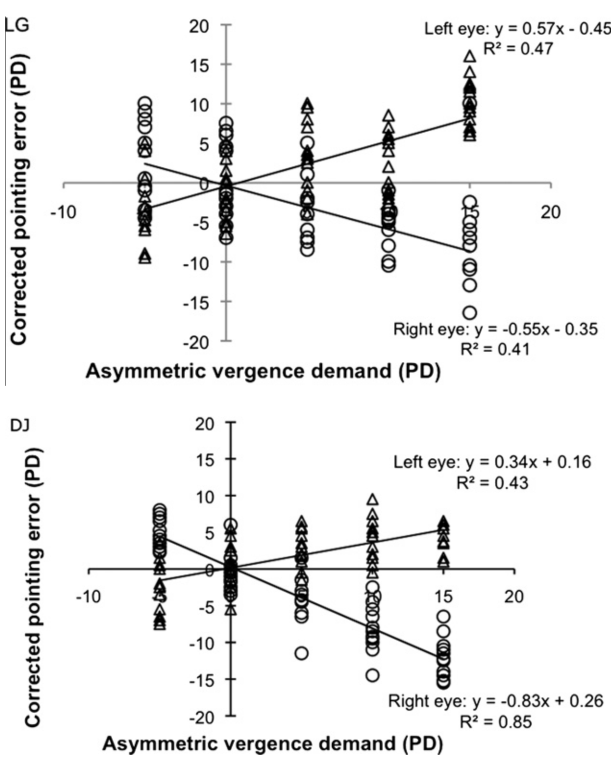

Fig. 1. Corrected pointing errors are plotted against the asymmetric vergence demand. Each plot shows the data of a single subject. Positive and negative values on the *x*-axis indicate convergence and divergence demands, respectively. Positive and negative numbers on the *y*-axis specify pointing errors toward the right and left, respectively. Each point represents one pointing response. The best fitting straight lines are shown for pointing responses during changes in the position of the left (triangles) and right eyes (circles). The equation and coefficient of determination is included for each fitted line.

3.3. Discussion

In this experiment, corrected pointing errors provided an estimate of the relative contribution of each eye's position information to *perceived* EVD. The variability of the pointing errors in this study is comparable to the average SDs of pointing errors between 2.6 and 5.2 PD reported previously by several authors (Barry, Bloomberg, & Heubner, 1997; Bedell, Klopfenstein, & Yuan, 1985; Bock & Kommerell, 1986; Gauthier, Berard, Deransard, Semmlow, & Vercher, 1985; Mann, Hein, & Diamond, 1979; Steinbach & Smith, 1981; Tadokoro, 1991). In agreement with the prediction from Hering's laws of visual direction and the results of previous studies (Barbeito & Simpson, 1991; Erkelens, 2000; Simpson, 1992), the eye-position information from both eyes contributes to *perceived* EVD during binocular viewing, as subjects made consistent pointing errors during asymmetric vergence in the direction of the converging or diverging eye's deviation.

The ratio of the absolute values of the slopes (RE/LE) provides an estimate of the magnitude of between-eye difference in the contribution of the eye-position information from the two eyes to *perceived* EVD. In particular, a ratio of 1 indicates an equal contribution of the eye-position information from the two eyes, and ratios more and less than 1 indicate a larger contribution of position information from the right and left eyes, respectively. In agreement with the previous report by Barbeito and Simpson (1991), we found significant between-eye differences in the pointing errors in some of the subjects. Specifically, some subjects' pointing errors changed more when the position of one eye was deviated compared to the other. This outcome is contrary to Hering's law of visual direction, which assumes that the eye-position information from both eyes contributes *equally* to the *perceived* EVD during binocular viewing. Rather, the results indicate that the extent to which eye-position information is taken into account depends in some subjects on the eye that makes the asymmetric vergence movement.

Barbeito and Simpson (1991) proposed that a difference in the contribution of eye-position information from the two eyes could occur either because the "hypothetical" cyclopean eye is shifted from a point between the two eyes towards one eye, or because of a difference in the weighting of the eye-position information from the two eyes. They distinguished between these alternatives by noting that the cyclopean eye could theoretically shift backward or forward from the corneal plane as well as laterally from the midpoint between the eyes, whereas a differential weighting of eye-position information is equivalent to only a lateral shift. However,

Table 1
Absolute values of slope (and 95% confidence intervals) fit to pointing errors as a function of the magnitude of asymmetric vergence, during right- and left-eyes deviations.

Subject	Slope RE[a]	Slope LE[a]	Ratio of Slopes (RE/LE)	Sum of slopes (RE + LE)
BN	**0.554 (0.448, 0.659)**[b]	**0.385 (0.295, 0.474)**[b]	**1.439 (1.007, 1.871)**[b]	0.939 (0.804, 1.073)
DJ	**0.835 (0.754, 0.916)**	**0.345 (0.253, 0.437)**	**2.420 (1.734, 3.107)**	1.180 (1.060, 1.300)
DN	**0.578 (0.478, 0.678)**	**0.308 (0.186, 0.429)**	**1.877 (1.068, 2.685)**	0.886 (0.731, 1.040)
DS	0.513 (0.449, 0.576)	0.417 (0.340, 0.493)	1.230 (0.958, 1.502)	0.930 (0.939, 1.036)
HB	**0.526 (0.468, 0.543)**	**0.693 (0.636, 0.754)**	**0.759 (0.675, 0.843)**	1.219 (1.139, 1.299)
JG	0.416 (0.341, 0.490)	0.488 (0.381, 0.596)	0.852 (0.613, 1.092)	0.904 (0.776, 1.032)
JQ	0.473 (0.401, 0.545)	0.456 (0.381, 0.530)	1.037 (0.806, 1.269)	0.929 (0.828, 1.030)
JW	**0.531 (0.461, 0.601)**	**0.348 (0.276, 0.420)**	**1.526 (1.152, 1.900)**	0.879 (0.779, 0.979)
KI	0.503 (0.380, 0.626)	0.637 (0.516, 0.758)	0.790 (0.613, 1.092)	1.140 (0.971, 1.309)
LG	0.548 (0.394, 0.701)	0.573 (0.432, 0.713)	0.956 (0.600, 1.312)	1.121 (0.917, 1.325)
NP	0.665 (0.587, 0.742)	0.576 (0.489, 0.663)	1.154 (0.937, 1.372)	1.241 (1.164, 1.317)
QL	**0.481 (0.358, 0.604)**	**0.158 (0.059, 0.257)**	**3.044 (1.012, 5.105)**	0.639 (0.518, 0.760)
TP	0.417 (0.251, 0.583)	0.420 (0.242, 0.599)	0.993 (0.415, 1.571)	0.837 (0.602, 1.071)
Subject DS[c]				
Trial 1	0.507 (0.409, 0.604)	0.482 (0.389, 0.576)	1.052	0.989 (0.856, 1.220)
Trial 2	0.519 (0.434, 0.603)	0.352 (0.235, 0.469)	1.474	0.861 (0.730, 1.010)
Subject HB[c]				
Trial 1	0.553 (0.464, 0.647)	0.661 (0.580, 0.741)	0.836	1.216 (1.096, 1.335)
Trial 2	0.493 (0.384, 0.602)	0.679 (0.562, 0.796)	0.726	1.176 (1.020, 1.331)

[a] Fitted slopes have negative and positive signs for asymmetric vergence deviations of the right and left eyes, respectively.
[b] Numbers in bold indicate a statistically significant difference between the absolute slope values fit to the data for the right and left eyes.
[c] Results obtained for two separate sets of trials for subjects are DS and HB are shown. The slopes shown for these subjects above were fit to the combined corrected pointing errors from the two sets of trials.

they concluded that these alternatives can not be distinguished readily from one another on the basis of experimental data. Their other suggestion, that between-eye differences in the weighting of eye-position information could occur as a result of a difference in the retinal input, is not supported by this experiment because in all subjects the best-corrected visual acuity was similar in the two eyes, identical targets of the same luminance and with essentially equal accommodative demand were presented to both eyes, and each subject's horizontal fixation disparity was approximately zero, such that in each eye the images of the target should have fallen very close to the fovea. The cyclopean eye is clearly a *theoretical* structure and there is still considerable controversy about its usefulness (Erkelens & van De Grind, 1994; Erkelens & van Ee, 2002; Ono, Mapp, & Howard, 2002). We conclude therefore that the between-eye differences exhibited by approximately half of the subjects in our study are better described in terms of idiosyncratic difference in the weighting of eye-position information, wherein the eye that is afforded more weight contributes more to the *perceived* EVD.

Despite significant between-eye differences in the contribution of eye-position information to *perceived* EVD, the absolute values of the slopes fit to the pointing errors for the left and the right eyes add to approximately 1 in most of the subjects in our study. A similar outcome can be deduced from the results of Barbeito and Simpson's (1991) study. In the context of Hering's law, this result suggests that a decrease in the weighting of one eye's position information is offset by an approximately commensurate increase in the weighting of the eye-position information from the other eye.

In Experiment 2, we address whether differences in weighting exist also for the contribution of the retinal information from each eye to *perceived* OVD.

4. Experiment 2: determination of the relative contribution of retinal information from the two eyes to perceived OVD

4.1. Experiment 2a: stimuli and methods

The stimuli consisted of a binocular fixation cross and dichoptic reference and test targets. The fixation cross had the same dimensions as the pointing target in Experiment 1. The reference and test targets were presented above and below the fixation cross, respectively, with a vertical edge-to-edge separation of 1.75°. The reference and the test targets were identical, each subtending 45 arc min in width by 53 arc min in height. Both of these targets had blurred vertical edges, produced by a one-dimensional Gaussian filter with a standard deviation of 8.0 arc min. When viewed through the ferro-electric goggles, the background luminance seen by each eye was 8 cd/m^2. The luminance of both the fixation cross and the reference targets was 12 cd/m^2, yielding a Weber contrast of 50%. The test target had either the same or different contrasts in the two eyes. Log contrast ratios other than 0 were achieved by decreasing the contrast of the test target in one eye and increasing it in the other eye, so that the mean contrast remained at 50%.

The fixation cross was presented separately to each eye with a horizontal separation that minimized each subject's horizontal fixation disparity. The upper reference target was presented with no horizontal retinal image disparity with respect to the fixation cross. The lower test target was presented with a horizontal binocular image disparity of 10.6 arc min (5.3 arc min for each eye), either in the crossed or uncrossed direction with respect to the fixation and the reference targets. During each block of 180 trials (90 trials each for the test target with crossed and uncrossed disparity), the test target was presented with one of six different log contrast ratios: −0.6, −0.3, 0, 0.3, and 0.6 (Left eye/Right eye). The contrast ratio chosen varied pseudorandomly from block to block. While keeping the horizontal binocular disparity constant, the *average* horizontal location of the dichoptic test target varied randomly from trial to trial between nine equally spaced horizontal locations, between 7.9 arc min to the right and 7.9 arc min to the left of the reference target.

The subject initiated each trial by fixating on the cross and pushing a button on the CT3 button box. The reference and the test targets then appeared simultaneously for 150 ms. During this presentation interval, the fixation cross disappeared, to minimize its ability to serve as an alignment cue. After each trial, the subject reported whether the fused test target appeared to the right or left of the reference target, using two other push buttons on the button box. The proportion of responses to the 'right' was tabulated separately for crossed and uncrossed disparities of the test target, and plotted against the nine horizontal locations at which the test target was presented. The values corresponding to 50% on the cumulative Gaussian functions that were fit to the crossed- and the uncrossed-disparity data gave an estimate of the lateral offsets (in arc min) at which the test and reference targets appeared in the same visual direction to the subject. These values will be referred to as the 'points of subjective equality' (PSEs). Positive and negative values of the PSE indicate that the test and reference targets were perceived to be in the same direction when the average direction of the test target was presented to the right and to the left of the reference target, respectively. Each subject repeated the experiment at least twice, either on the same or on a different day.

The PSEs determined for the test targets with crossed and uncrossed disparity were plotted against the log of the contrast ratios. Straight lines that minimized the sum of the squared errors were fit separately to the crossed- and uncrossed-disparity data. The intersection of these two straight lines indicated the log contrast ratio at which the fused lines with crossed and uncrossed disparity were perceived to be aligned. The log contrast ratio that yielded alignment of crossed- and uncrossed-disparity targets was obtained also using a model fit, as described below in Section 4.8.

4.2. Experiment 2b: stimuli and methods

To measure perceived OVD for targets with different *luminance* ratios in the two eyes, the following alterations were made to the experimental set-up from Experiment 2a. The room in which the experiment was carried out was kept completely dark to eliminate any visible frame of reference. The luminance of the display monitor was approximately zero and the luminance of the fixation cross and the reference target seen by each eye was 2.5 cd/m^2. During each block of 180 trials, the log interocular luminance ratio of the dichoptic test target was −1.2, −0.6, −0.3, 0, 0.3, 0.6 or 1.2, while the mean luminance of the targets seen by the two eyes was maintained at 2.5 cd/m^2. The log luminance ratio at which the two straight lines fit to the PSEs for crossed- and uncrossed-disparity targets intersected was obtained as in Experiment 2a.

4.3. Experiment 2c: stimuli and methods

Hariharan-Vilupuru and Bedell (2009) suggested that horizontal and vertical disparities may exert different effects on the perceived direction of monocular line targets (reference and test targets) surrounded by binocular random dot stereograms for monocular target separation less than approximately 3°. To address this possibility for binocular targets, 10 subjects repeated Experiment 2a using targets with vertical retinal image disparity. To measure the perceived OVD for targets with vertical disparity, horizontal reference and test targets were presented to the left and right of the fixation cross, respectively, with a horizontal edge-to-edge separation of 1.75°. The reference target was presented with no vertical image disparity, and the test target was presented with either right-hyper or left-hyper disparity of 10.6 arc min. The rest of the experimental set-up, methods and analysis were identical to Experiment 2a, except that positive and negative values of the PSE indicate that the test and the reference targets were perceived to be in the same direction for test targets with right-hyper and left-hyper disparities, respectively.

4.4. Results: experiment 2

Fig. 2a and b shows the PSEs of one subject and the best-fit straight lines to the data obtained for targets with crossed and uncrossed disparity with different interocular contrast and luminance ratios. Fig. 2c shows data for the same subject, for targets with right-and left-hyper disparities and different interocular contrast ratios. The intersection points of the two straight lines fit to each subject's data are tabulated in the leftmost column of Table 2, along with the 95% confidence intervals for the intersection points, obtained by bootstrapping. In four of the 13 subjects (DJ, DN, JQ, and QL), the fitted lines intersect at a log contrast ratio that is significantly greater than 0, indicating that the targets with crossed and uncrossed disparities were perceived in the same direction when the left eye's image had higher contrast. In the rest of the subjects, the log contrast ratio that yielded perceived alignment for the targets with crossed and uncrossed disparity did not differ significantly from equal contrast in the two eyes. Across the 13 subjects, the log contrast ratio that yielded perceived alignment of the crossed- and the uncrossed-disparity targets ranged from −0.05 to 0.43, with a median value of 0.07 log units.

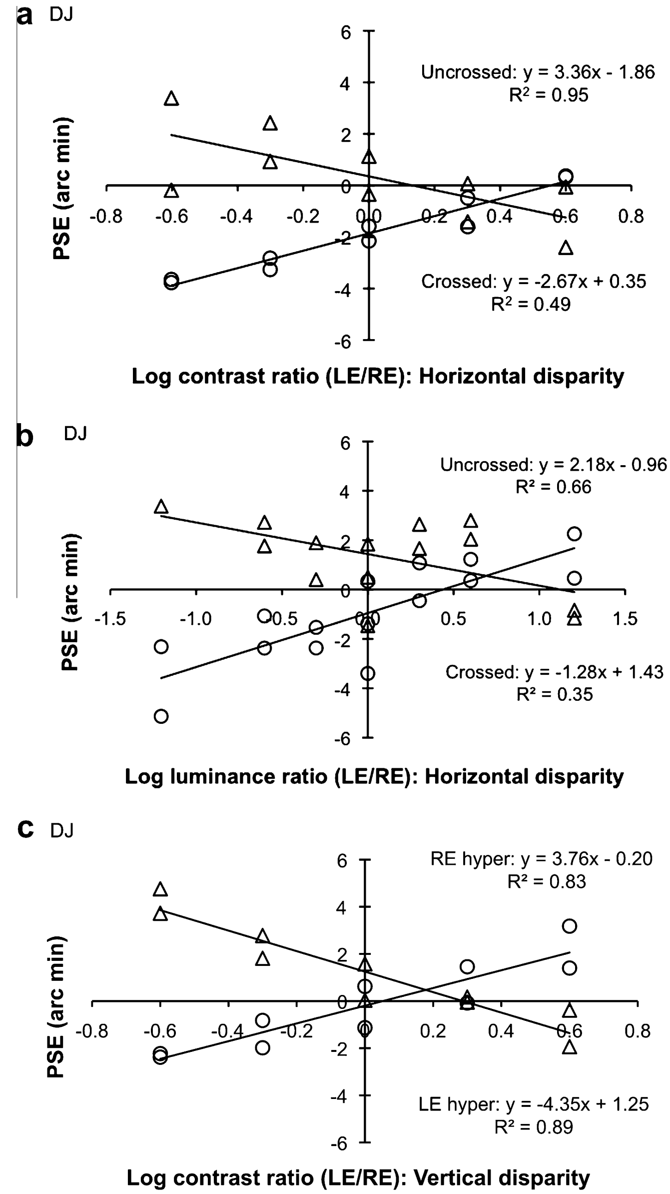

Fig. 2. Points of subjective equality (PSEs) are shown for one subject for (a) different interocular log contrast ratios for horizontally disparate targets (b) different interocular log luminance ratios for horizontally disparate targets and (c) different interocular log contrast ratios for vertically disparate targets. In panels (a) and (b), the triangles and circles indicate PSEs on one set of trials for test targets with crossed and uncrossed disparity, respectively. In panel (c), the triangles and circles are PSEs for left-hyper and right-hyper disparity, respectively. The equation and coefficient of determination is included for each fitted line.

Table 2
Log contrast ratio and log luminance ratios (and 95% confidence intervals) at which the lines fit to visual direction matches for crossed and uncrossed-disparity targets intersect.

Subject	Horizontal disparity log contrast ratio	Horizontal disparity log luminance ratio	Vertical disparity log contrast ratio
BN	0.055 (−0.055, 0.166)[a]	**0.356 (0.147, 0.714)**[a]	**0.062 (0.001, 0.125)**[a]
DJ	**0.368 (0.161, 0.605)**	**0.690 (0.244, 1.191)**	**0.178 (0.059, 0.316)**
DN	**0.430 (0.233, 0.745)**	0.376 (−0.064, 0.881)	**0.182 (0.075, 0.295)**
DS	0.112 (−0.025, 0.262)	0.155 (−0.150, 0.516)	**0.233 (0.194, 0.271)**
HB	0.070 (−0.381, 0.689)	−0.196 (−1.161, 0.608)	**0.069 (0.017, 0.124)**
JG	−0.055 (−0.142, 0.030)	−0.072 (−0.223, 0.086)	−0.024 (−0.104, 0.061)
JQ	**0.284 (0.072, 0.542)**	0.145 (−0.043, 0.318)	–
JW	0.057 (−0.048, 0.170)	**1.854**	–
KI	−0.028 (−0.169, 0.123)	−0.256 (−0.684, 0.142)	0.018 (−0.082, 0.108)
LG	0.070 (−0.090, 0.216)	–	**−0.066 (−0.139, −0.001)**
NP	0.072 (−0.062, 0.216)	0.097 (−0.270, 0.359)	−0.020 (−0.072, 0.028)
QL	**0.172 (0.076, 0.272)**	**0.258 (1.032, 3.448)**	–
TP	−0.007 (−0.151, 0.106)	**0.366 (0.117, 0.624)**	**0.021 (0.002, 0.204)**

[a] Bold symbols indicate subjects with log contrast or log luminance ratios that differ significantly from zero, indicating a significant between-eye difference in weighting.

For targets that differed in *luminance* in the two eyes, five subjects (BN, DJ, JW, QL and TP) required significantly higher luminance of the left eye's image for the targets with crossed and uncrossed disparities to be perceived as aligned (Table 2, center column). For the subject with anisometropia (JW), the crossed- and uncrossed-disparity targets had a log luminance ratio of 1.85 when the two targets were perceived to be aligned.[2] For the rest of the 11 subjects, the log luminance ratio that yielded perceived alignment of the crossed- and the uncrossed-disparity targets ranged from −0.26 to 0.69, with a median value of 0.17 log units.

The rightmost column in Table 2 shows that the targets with *vertical* disparity were seen as aligned when the left eye had significantly higher contrast in six of the 10 subjects, and when the right eye had higher contrast in one subject. The median log contrast ratio that produced perceived alignment was 0.06, with a range between −0.07 and 0.23 log units.

As seen in Fig. 2, the lines fit to the data for crossed and uncrossed (or right- and left-hyper) retinal-image disparities sometimes intersected above or below 0 arc min on the *y*-axis. We interpret these offsets of the intersection points from the *x* axis as constant errors of alignment, as have been reported previously in normal observers for separated Vernier targets (e.g., Bedell, Flom, & Barbeito, 1985; French, 1920).

For 11 of the subjects who performed the OVD experiments with targets that differ in both contrast and luminance, orthogonal regression (Minitab 16 statistical software) revealed a significant relationship between the log contrast and the log luminance ratios that produced perceived alignment for targets with crossed and uncrossed horizontal retinal-image disparities (95% confidence intervals (CI) for the slope = 0.30–3.12; $r = 0.63$[3], 95% CI = 0.04–0.89, $p = 0.04$). This relationship, shown in Fig. 3, excludes the data of subject JW with anisometropia, whose log luminance ratio to produce perceived alignment for targets that varied in luminance is clearly an outlier. A statistically significant relationship also exists between the log contrast ratios that produced perceived alignment for targets with horizontal and vertical image disparities (95% CI for the slope = 0.17–1.08; $r = 0.69$, 95% CI = 0.11–0.92, $p = 0.03$, Fig. 4). As indicated by their confidence intervals, the slopes of the regression lines in Figs. 3 and 4 do not differ significantly from 1.

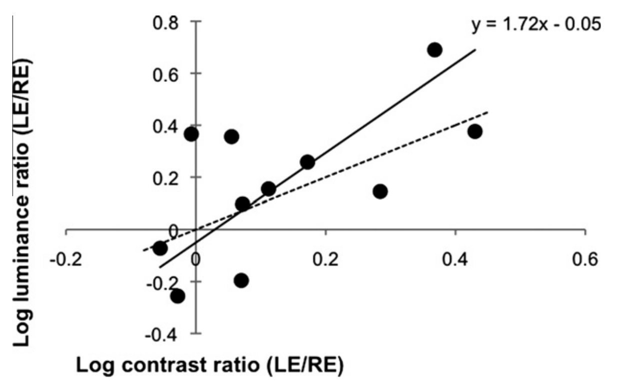

Fig. 3. Comparison between the relative weighting of retinal information, as estimated using targets with different log contrast ratios (*x* axis) and log luminance ratios (*y* axis) in the two eyes. Each data point represents the results of one subject. The dashed line specifies perfect agreement. The solid line is the best fit to the data.

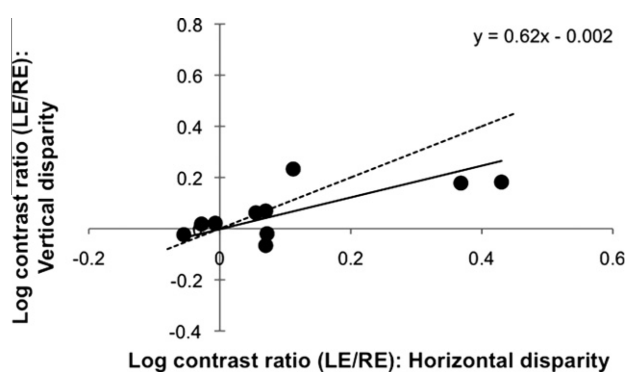

Fig. 4. Comparison between the relative weighting of retinal information, as estimated using targets with different interocular contrast ratios with horizontal (*x* axis) and vertical disparity (*y* axis). The dashed and solid lines are as in Fig. 3.

4.5. Effects of varying test-target disparity and induced fixation disparity on OVD

It is possible that the observed shifts of the PSE in Experiment 2 toward the target with higher contrast (or luminance) occur because the disparity of ±10.6 arc min was too large for the observers to fuse. In particular, observers could have reported alignment when the center of the two overlapping monocular images of the test target was aligned with the fused image of the reference

[2] Subject JW performed the experiment twice. On two individual trials, the log luminance ratios required to produce perceived alignment were 2.07 and 1.72.

[3] The values of *r* and the associated CIs reported for the relationships shown in Figs. 3–5 were determined by Pearson product–moment correlation.

target. Although this scenario is unlikely, subject DS repeated the experiment for targets with different contrast ratios and crossed and uncrossed horizontal disparities of 5.3 and 15.8 arc min. This manipulation produced a systematic change in the slopes of the lines fit to the crossed- and uncrossed-disparity data. The slopes of the lines fit to the PSEs for the targets with crossed and uncrossed disparity were averaged (neglecting sign) and plotted against the test-target disparity. A best-fit line was obtained, with a slope equal to 0.3 times the test-target disparity ($r = 0.99$). Most importantly, the relative weighting of the retinal information from this subject's two eyes (log values of 0.09 and 0.04) remained similar to the value obtained using targets with ±10.6 arc min of disparity (log value of 0.11).

A second control experiment was performed on two subjects to assess the effect of vergence posture on the weighting of retinal information for targets with different contrast ratios in the two eyes. Vergence demands between 8 PD BO and either 12 PD or 20 PD BI (determined with respect to the distance of the monitor) generated fixation disparities between 8.7 arc min exo and 7.3 arc min eso in one subject, and between 13.5 arc min exo and zero in the other subject. As the direction of fixation disparity changed from exo to eso, there was a decrease in slopes of the lines fit to the PSEs for crossed- disparity targets and an increase in slopes for uncrossed-disparity targets. Despite the sizable changes in fixation disparity, and in the slopes of the best-fit straight lines, neither subject exhibited a systematic variation in the estimated weighting of retinal information (range of log contrast ratios = 0 to −0.26 in subject HB and 0.21 to 0.02 in subject DS).

4.6. Precision of direction judgments

The precision of the subjects' direction judgments was obtained from the slopes of the psychometric functions fit to the PSEs for crossed- and uncrossed-disparity targets in Experiments 2a and 2b, and for the right- and left-hyper disparity targets in Experiment 2c. Across the subjects who performed the OVD experiment for horizontally disparate targets, the average slopes were 2.71 ± 1.05 and 2.64 ± 1.14 arc min for contrast- and luminance-varying targets, respectively. The average slope for the 10 subjects who performed the experiment with vertically disparate, contrast-varying targets was 2.40 ± 1.04 arc min. The difference between the slopes for the contrast- and luminance-varying targets, and for the contrast-varying targets with horizontal and vertical disparities was not significant statistically.

4.7. Discussion

In agreement with Mansfield and Legge (1996) and Francis and Harwood (1951), we found a systematic shift in the *perceived* OVD of a target presented with *different* interocular contrast or luminance ratios towards the eye that views the image of higher contrast or luminance, regardless of whether the target was presented with horizontal or vertical disparity. If the width of our bar target is considered to represent one half cycle of a grating, then the corresponding fundamental spatial frequency is equal to 0.67 cpd. The maximum absolute values of the PSEs that we found using bar targets are quantitatively comparable to those obtained by Mansfield and Legge (1996) for a 1 cpd Gabor grating presented with 10 arc min of horizontal disparity. However, our PSEs are smaller than the maximum PSEs of approximately 10 arc min reported by Ding and Sperling (2006, 2007) using 0.68 cpd targets with 11 arc min of vertical retinal image disparity.

We believe that the perceived direction of the horizontally and vertically disparate targets in this study represents the direction of the *fused* binocular image, rather than the direction of one eye's image during suppression of the opposite eye, as might occur because of interocular contrast or luminance differences or because of the large disparity of the test target. Evidence for fusion comes from an analysis of the subjects' psychometric functions. If the retinal information from either the left (or right) eye were constantly suppressed, then a test target with 10.6 arc min crossed disparity should have been seen consistently to the left (or right) of the reference target, at least up to an offset equal to half the test target's retinal image disparity. However, the subjects had PSEs that were less than the monocular component of the target's disparity: the average *maximum* unsigned PSEs for all subjects were 4.11 ± 0.29, 4.09 ± 0.31 and 4.52 ± 0.30 arc min (Mean ± SE) respectively, for contrast- and luminance-varying targets with horizontal disparity, and for contrast-varying targets with vertical disparity. PSEs that are smaller than the monocular component of disparity were obtained even when the target disparity was increased to 15.9 arc min in the control experiment (Maximum unsigned PSE = 7.46 arc min) that was described in Section 4.5, above. Another alternative to fusion is that the retinal information from the two eyes was suppressed alternately, in which case the slope of the psychometric functions for each of the interocular contrast and luminance ratios should have been shallow, on the order of 5 arc min. In contrast to this expectation, the slopes of the psychometric functions were similar to those reported previously for non-dichoptically viewed low spatial frequency targets (e.g., Bradley & Skottun, 1987; Chung & Bedell, 2003; McKee & Levi, 1987; Toet & Koenderink, 1988; Whitaker et al., 2002). The relatively brief target duration in our study contains high temporal frequency information (Yang & Stevenson, 1997), which might be expected to reduce the extent of Panum's fusional area (Schor & Tyler, 1981). Nevertheless, our subjects did not report diplopia.

For between one and two thirds of the observers that we tested, the straight lines fit to the PSEs for targets with opposite directions of horizontal or vertical disparity intersect at a log contrast or luminance ratio that differs significantly from 0. We interpret these log contrast and luminance ratios to indicate the magnitude of between-eye differences in the weighting of retinal information from the two eyes. An intersection of the lines at a log contrast or luminance ratio of zero indicates that targets with opposite directions of disparity are seen in the same direction when the image contrast or luminance in both eyes is equal, which implies that the retinal information from both eyes is weighted equally. The intersection of the two lines at a ratio larger (or smaller) than zero indicates that targets with opposite directions of disparity are seen in the same direction when the image in the left (or the right) eye has a higher contrast or luminance, which suggests a greater weighting of the image from right (or the left) eye. In contrast to the assumption made by Hering's law, the results indicate that the retinal information from the two eyes does not contribute equally to perceived OVD in all subjects.

Banks, van Ee, and Backus (1997) suggested that small vergence errors could affect the perceived OVD of binocularly disparate targets. In the current experiment, the *slopes* of the lines fit to the PSEs for the crossed- and the uncrossed-disparity data are expected to be equal in the absence of a fixation disparity and unequal in the presence of fixation disparity. Assume that the left and right eyes of a subject contribute equally to perceived OVD when the images in each eye have the same contrast. In addition, assume that the subject has an exo-fixation disparity that is equal to the disparity of the test target. Because of the fixation disparity, the zero-disparity fixation cross and reference target will fall on non-corresponding points (projected to the right of the fovea for the left eye, and to the left of the fovea for the right eye) rather than on corresponding *foveal* points. However, because the images of the reference target are presented with equal contrast in the two eyes, the fused reference target will always be perceived in the same, veridical direction.[4] The observer's exo-fixation disparity will cause the test target with uncrossed disparity to fall on corresponding foveal points. Therefore, it too always should be perceived in its veridical direction, regardless of the interocular contrast ratio. If the reference and uncrossed-disparity test targets are seen in the same direction regardless of the interocular contrast ratio, then the straight line fit to the uncrossed PSEs should have a slope of zero. For the crossed disparity test target, exo-fixation disparity will cause the left- and right-eye images to be projected more to the right and the left, respectively, than the reference targets in the same eyes. However, unlike the reference target, the perceived direction of the test target should shift according to the interocular contrast ratio, producing larger changes in the PSE than in the absence of fixation disparity, and therefore an increase in the slope of the best-fit straight line. Note, however, that the intersection between the straight lines fit to the uncrossed and crossed disparity data should be unaffected by fixation disparity, as the lines will cross at the interocular contrast ratio that yields equal weighting of the left and right eyes' retinal information.

Changes in the slope, but not in the intersection point, of the straight lines fitted to the PSE data were observed when fixation disparity was introduced by displacing the targets on the monitor in the control experiment described in Section 4.5. Nevertheless, we minimized each subject's fixation disparity during the main experiment. In addition, the test targets were presented randomly on each trial with either crossed or uncrossed disparity, to minimize the likelihood of predictive vergence eye movements (Kumar, Han, Garbutt, & Leigh, 2002; Yuan, Semmlow, & Munoz, 2000). To further minimize the possibility that the vergence posture would change, the duration of the test and reference targets was less than the latency of vergence (Krishnan, Farazian, & Stark, 1973; Rashbass & Westheimer, 1961). Therefore, it is unlikely that the results of this study were affected to any meaningful extent by the presence of fixation disparity or by vergence eye movements.

Heinrich, Kromeier, Bach, and Kommerell (2005) reported that that the ocular prevalence (a term for a preference given to the targets seen by one eye, when the targets are located close to the horopter) estimated from stereothresholds varies with the disparity of the binocular target for small disparities. In contrast, we found that between-eye differences in the weighting of retinal information remain approximately the same for test target disparities between 5 and 15 arc min, at least as determined in subject DS. The slopes of the lines fit to the PSEs for crossed- and uncrossed-disparity targets with different interocular log contrast ratios increased linearly as a function of horizontal disparity of the test target, as expected from the geometry of the viewing conditions. Our finding of no apparent change in the weighting of retinal information for targets with different horizontal disparities is consistent with the observation by Sheedy and Fry (1979) that the same eye was "dominant for directionalization" for the range of vertical target disparities that they used (2–6 arc min).

The relative weighting of retinal information determined for each subject for pairs of horizontally disparate targets with different contrast and luminance ratios, and for vertically disparate targets with different contrast ratios generally are in agreement (Table 2). However, agreement between the relative weighting for targets of different contrast and luminance did not occur for all of the subjects. Specifically, the data of subject JW with anisometropia indicate only a small between-eye difference in the weighting of retinal information for stimuli that differ in contrast, but a substantially larger difference in weighting for stimuli that differ in luminance. If this result were confirmed in additional subjects, it would raise the possibility that two monocular images with unequal contrast or luminance are combined differently to determine the perceived OVD of the binocular image. Because a similar relative weighting of the retinal information from the two eyes occurs for horizontally and vertically disparate targets, we conclude that perceived OVD is not influenced substantially by the perception of stereoscopic depth.

4.8. Modified Ding and Sperling model

Ding and Sperling (2006, 2007) presented vertically disparate gratings of unequal contrast to the two eyes and asked their observers to specify the perceived location of the fused binocular grating. Their results provide evidence for a model in which the perceived location of the binocular grating is based on a *nonlinear* summation of the image contrast in the two eyes. Specifically, Ding and Sperling proposed that a high contrast image in one eye produces a relative attenuation of the contrast information from the other eye. This interactive gain control is incorporated into their model by applying exponents greater than one to the two monocular image contrasts. Ding and Sperling eliminated possible between-eye differences in the weighting of monocular images with different contrasts by averaging the results obtained for gratings with opposite phase relationships in the left and right eyes.

We modified the Ding and Sperling model to include relative weighting of the retinal information from the two eyes and an idiosyncratic constant error. In addition, we fixed the disparity of the test target at 10.6 arc min. According to this modified model, the predicted PSE can be calculated as follows:

$$\text{Predicted PSE} = \frac{D_L \times C_L^g \times W_L + D_R \times C_R^g \times W_R}{C_L^g \times W_L + C_R^g \times W_R} + \text{constant error} \quad (1)$$

where D_L and D_R are the offsets of the target with respect to the fixation point in the left and right eyes (i.e., one half of the total binocular disparity in each eye, in arc min), W_L and W_R are the weighting of the retinal information in left and right eyes (where $W_R = 1 - W_L$), and C_L and C_R are the contrasts of the test target that are presented to the left and right eyes. The *effective* contrast of the test target shown to the left and the right eye is estimated by raising the physical contrast of the target to the exponent, 'g'. The parameters that were free to vary are the weight given to the retinal information from the left eye, the exponent g, and the constant error.[5] The fminsearch function in MATLAB varied these free parameters to produce a fit that minimized the sum of the squared errors in the measured data. Ratios of the weights (W_R/W_L), that are greater or less than 1 indicate that the retinal information from the right or the left eye, respectively, contributes more to *perceived* OVD.

Applying the modified Ding and Sperling model to our results, the relative weighting obtained for targets of different *contrast* in the two eyes ranged from −0.03 to 0.26 log units, with a median value of 0.03 log units. Across subjects, the value of the fitted exponent 'g' ranged from 0.32 to 0.71, with a median value of 0.57. For targets of difference *luminance* in the two eyes, the between-eye difference in weighting for the eleven subjects tested ranged from −0.03 to 0.19 log units with a median value of 0.05 log units. The value of the fitted exponent 'g' ranged from 0.10 to 0.34 with a median value of 0.26.

[4] If the observer weights the retinal information from one eye more than the other, then the reference target always will be seen in the same non-veridical direction. Otherwise, the rest of the following discussion is unchanged.

[5] The equation for the modified Ding and Sperling model is very similar to the expression used by Mansfield and Legge (1996) to predict the perceived direction of a binocular target. However, in the equation proposed by Mansfield and Legge the exponent specifies the variation in visual-direction sensitivity with target contrast, and is not a free parameter in the model. The values of the fitted exponents that we obtained for targets with different inter-ocular contrast ratios are similar to the values obtained empirically by Mansfield and Legge.

For 10 of the 13 subjects who viewed horizontally disparate targets of different contrast, and for all 11 subjects (excluding JW) who viewed targets of difference luminance in the two eyes, the straight line fit accounted for a larger percentage of variance than the modified Ding and Sperling model. One possible explanation for the generally higher coefficients of determination obtained with the straight-line fits is that, unlike the modified Ding and Sperling model, the straight-line model does *not* assume that the PSEs for crossed and uncrossed disparities change reciprocally. Another possible explanation is that the straight-line fits do not require the PSEs to asymptote at a value equal to one-half of the target disparity, as the modified Ding and Sperling model does. Finally, the fitting of two straight lines involves four free parameters, compared to only three free parameters in the modified Ding and Sperling model.

Ding and Sperling (2006, 2007) reported values of the exponent g that ranged from 1.18 to 2.27 for their three subjects, consistent with a reduction of the response gain in each eye based on the contrast of the target presented to the other eye. The values of the exponent, g, that we obtained using our modified version of the Ding and Sperling model are considerably lower. The apparent reason for the lower values of exponent in our study is that our subjects' PSEs are much smaller than the phase shifts that Ding and Sperling obtained for gratings with high interocular contrast ratios. In particular, the Ding and Sperling model assumes that the PSE should asymptote to the magnitude of the target disparity at the largest contrast ratios.

Despite these differences, the modified Ding and Sperling model predicts that the retinal information from the left eye is given more weight than that from the right eye (and vice versa) in the same subjects as the straight-line fits, both for targets that differ in contrast and in luminance.

In the next set of experiments, we determined how these measures of weighting relate to ocular dominance, measured using three different tests.

5. Comparison with measures of ocular dominance

5.1. Stimuli and methods

Ocular dominance was measured by a sighting task and two sensory tasks in subjects who participated in Experiments 1 and 2. The dominant eye for sighting was defined as the eye the subject used to view a 20/40 Snellen letter, seen at a distance of 20 ft. through a 3 cm diameter circular hole in an opaque card (Hole-in-the-card test). Each subject repeated the task four times. As one measure of *sensory* ocular dominance, we compared the monocular contrast detection thresholds for the reference target (a vertical line with blurred edges) that was used to measure perceived OVD in Experiment 2a. This target was enclosed within a square fixation cross (53 × 53 arc min) to aid in detection. The other measure of *sensory* dominance was a variation of the blur-suppression test described by Schor, Landsman, and Erickson (1987). The target consisted of a dichoptic cross identical to the cross used for pointing in Experiment 1. This cross was enclosed within a 1.1° × 1.1° square that served as a fusion lock. The cross presented to one eye had 50% Weber contrast and was unblurred. The cross presented to the other eye was blurred by a two-dimensional Gaussian filter that generated a point spread function (PSF) with a full width at half height of 20.6 arc min. This width of the PSF is equivalent to that produced by 1.50 D of spherical dioptric blur for a 4 mm pupil diameter (Smith, Jacobs, & Chan, 1989). Subjects altered the contrast of the monocularly blurred target using the method of adjustment, so that the fused target just appeared to be clear. For both the contrast detection and the blur-suppression tests, the monocular target and the blurred cross, respectively, were presented to each eye four times and the thresholds from each set of four trials were averaged. The direction (right or left eye) and magnitude of eye dominance were estimated from the ratio of the thresholds when the left vs. the right eye viewed the monocular or the blurred target. Specifically, a ratio of 1 indicates equal dominance, and ratios greater and lesser than 1 indicate right eye and left eye dominance, respectively.

5.2. Results and discussion

Each subject used the same eye consistently for sighting on the four trials of the hole-in-the card test. Ocular dominance, determined quantitatively as the log ratio of the contrast-detection and blur-suppression thresholds in the two eyes, ranged across subjects from −0.27 to 0.30 and from −0.62 to 0.25 log units, respectively. These two measures of sensory dominance do not exhibit a significant correlation ($r = -0.46$, $p = 0.16$).

Table 3 compares the qualitative agreement between the three different measures of eye dominance and the weighting of eye-position and retinal information that were determined in Experiments 1 and 2. As can be seen in the table, the direction of eye dominance (right or left) did not agree consistently with the eye that was given higher weighting for eye-position or retinal information. In addition, orthogonal regression failed to show a significant quantitative relationship between the log contrast-detection ratio and the log weighting of eye-position or retinal information for either contrast- or luminance-varying targets (range of r values = −0.52 to −0.27). On the other hand, a significant positive relationship exists between the log blur-suppression threshold ratios and the weighting of retinal information as determined for luminance-varying targets ($r = 0.69$, $p = 0.028$). Similar positive relationships exist between the log blur-suppression threshold ratios and the log weighting of eye position and retinal information determined for horizontally and vertically disparate contrast-varying targets, but none of these relationships achieve statistical significance ($r = 0.52$ for all three comparisons). In general, these results are consistent with several previous reports that different measures of ocular dominance do not agree qualitatively or

Table 3
Percentage of subjects displaying agreement between different measures of ocular dominance and eye-position and retinal information weighting. Values in parentheses indicate the number of subjects who exhibited agreement/number of subjects for each comparison.

		Hole-in-the-card	Contrast sensitivity	Monocular blur suppression
Eye-position weighting		61 (8/13)	54 (6/11)	64 (7/11)
Retinal information weighting	Contrast Horizontal Disparity	61 (8/13)	55 (6/11)	54 (6/11)
	Luminance Horizontal disparity	64 (7/11)	60 (6/10)	50 (5/10)
	Contrast Vertical disparity	60 (6/10)	56 (5/9)	56 (5/9)

Note. Subject JW with anisometropia was classified as an outlier in the experiment on the weighting of retinal information for luminance-defined targets. Consequently, her data are not included in the table for the comparisons between eye dominance and the relative weighting of retinal information for targets of different luminance. JW exhibited right-eye dominance on each of the three eye-dominance tests, in agreement with her results for relative weighting of eye position and retinal information (Tables 1 and 2).

quantitatively with one other (Li et al., 2010; Pointer, 2007; Porac & Coren, 1976, 1986; Rice, Leske, Smestad, & Holmes, 2008; Robboy, Cox, & Erickson, 1990; Suttle et al., 2009; Walls, 1951).

In the next section, we determined whether the contribution of eye-position and retinal information from the two eyes vary similarly within the same subjects.

6. Comparison of relative contributions of eye-position and retinal information

The ratio of the slopes in Table 1 were converted from linear to logarithmic units to foster comparison of between-eye differences in the weighting of eye-position information from Experiment 1 and the weighting of retinal information from Experiments 2a, 2b and 2c. Fig. 5a–c compares the relative weighting of eye-position information and retinal information for horizontally disparate targets with different log interocular contrast and luminance ratios, and vertically disparate targets with different log interocular contrast ratios, respectively.

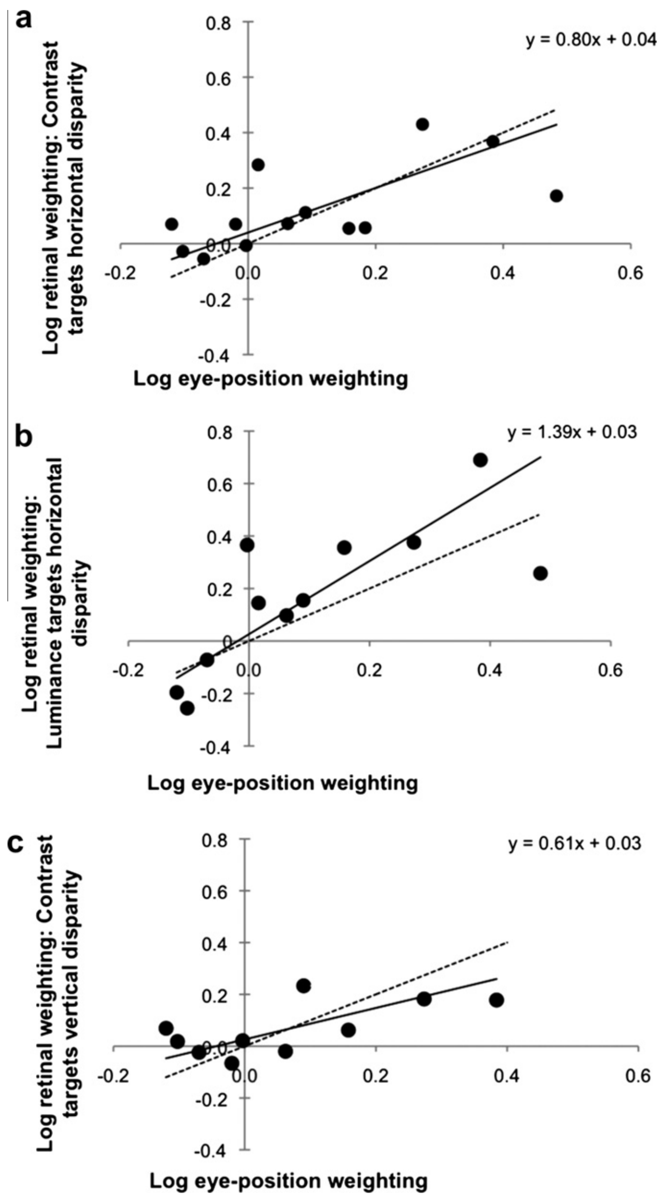

Fig. 5. Comparison between the relative weighting of eye-position (*x* axis), as determined from pointing responses, and the relative weighting of retinal information, estimated using (a) horizontally disparate targets with different contrast in the two eyes, (b) horizontally disparate targets with different luminance in the two eyes, and (c) vertically disparate targets with different contrast in the two eyes. The relative weighting of eye position is specified as the log ratio of the slopes fit to the results when the right and left eye positions varied. The relative weighting of retinal information is given as the log interocular contrast or luminance ratio that resulted in perceived alignment between targets with crossed and uncrossed (or right and left hyper) disparity. In each panel, the dashed and solid lines have the same significance as in Fig. 3.

For the 13 subjects who participated in Experiment 2a and the 10 subjects who participated in Experiment 2c, the relationship between the weighting of the eye-position and retinal information for targets of different contrast was statistically significant (for horizontally disparate targets, 95% confidence intervals for slope: 0.21, 1.39; $r = 0.63$, 95% CI = 0.12–0.88, $p = 0.02$, Fig. 5a; for vertically disparate targets, 95% CI for slope = 0.11, 1.10; $r = 0.65$, 95% CI = 0.04–0.91, $p = 0.04$, Fig. 5c). Similarly, the relationship between the relative weighting of eye-position information and retinal information for targets of different luminance for the 11 subjects from Experiment 2b (excluding JW) also is significant (95% CI for slope = 0.85, 2.12; $r = 0.76$, 95% CI = 0.29–0.93, $p = 0.007$, Fig. 5b).

A number of previous experiments on binocular visual direction (Barbeito & Simpson, 1991; Charnwood, 1949; Francis & Harwood, 1951; Hariharan-Vilipuru & Bedell, 2009; Mansfield & Legge, 1996; Ono & Weber, 1981; Verhoeff, 1933) assumed that the relative weighting of eye-position and retinal information from the two eyes is similar in the same subjects. The results of our experiments show that the contributions of the two eyes to eye-position and retinal information *do* vary similarly between the two eyes in most subjects.

7. Conclusions

In contrast to the predictions made by Hering's law of visual direction, the eye-position and retinal information from the two eyes do not contribute equally to perceived egocentric visual direction in all subjects. However, the relative contributions of eye-position and retinal information are similar in most subjects. Because similar relative weighting of retinal information is found using horizontally and vertically disparate targets, the determination of perceived OVD does not depend substantially on perceived stereoscopic depth. Different estimates of ocular dominance do not agree with the relative weighting of eye-position or retinal-image information, or with each other. These results in subjects with normal binocular vision lay the groundwork for understanding how information about visual direction from the two eyes is combined in the presence of abnormal binocular vision, such as in subjects with strabismus.

Acknowledgments

This research was supported by Core Grant NIH P30 EY07551 to the College of Optometry University of Houston, and a University of Houston Vision Research Student Grant.

References

Banks, M. S., van Ee, R., & Backus, B. T. (1997). The computation of binocular visual direction: a re-examination of Mansfield and Legge (1996). *Vision Research, 37*, 1605–1610.

Barbeito, R., & Ono, H. (1979). Four methods of locating the egocenter: A comparison of their predictive validities and reliabilities. *Behavior Research Methods & Instrumentation, 11*, 31–36.

Barbeito, R., & Simpson, T. L. (1991). The relationship between eye position and egocentric visual direction. *Perception & Psychophysics, 50*, 373–382.

Barry, S. R., Bloomberg, J. J., & Heubner, W. P. (1997). The effect of visual context on manual localization of remembered targets. *Neuroreport, 8*, 469–473.

Bedell, H. E., Flom, M. C., & Barbeito, R. (1985). Spatial aberrations and acuity in strabismus and amblyopia. *Investigative Ophthalmology & Visual Science, 26*, 909–916.
Bedell, H. E., Klopfenstein, J. E., & Yuan, N. (1985). Extraretinal information about eye position during involuntary eye movement: Optokinetic afternystagmus. *Perception & Psychophysics, 46*, 579–586.
Blouin, J., Amade, N., Vercher, J., Teasdale, N., & Gauthier, G. M. (2002). Visual signals contribute to the coding of gaze direction. *Experimental Brain Research, 144*, 281–292.
Bock, O., & Kommerell, G. (1986). Visual localization after strabismus surgery is compatible with the "outflow" theory. *Vision Research, 11*, 1825–1829.
Bradley, A., & Skottun, B. C. (1987). Effects of contrast and spatial frequency on vernier acuity. *Vision Research, 27*, 1817–1824.
Bridgeman, B. (1995). A review of the role of efference copy in sensory and oculomotor control systems. *Annals of Biomedical Engineering, 23*, 409–422.
Bridgeman, B., & Stark, L. (1991). Ocular proprioception and efference copy in registering visual direction. *Vision Research, 31*, 1903–1913.
Buisseret, P., & Maffei, L. (1977). Extraocular proprioceptive projections to the visual cortex. *Experimental Brain Research, 28*, 421–425.
Charnwood, J. R. B. (1949). Observations on ocular dominance. *The Optician, 116*, 85–88.
Charnwood, J. R. B. (1965). Binocular space perception. In *An Essay on binocular vision* (pp. 89–110). New York: Hafner Publishing Co.
Chung, S., & Bedell, H. E. (2003). Velocity dependence of Vernier and letter acuity for band-pass filtered moving stimuli. *Vision Research, 43*, 669–682.
Ding, J., & Sperling, G. (2006). A gain-control theory of binocular combination. *Proceedings of the National Academy of Sciences of the United States of America, 103*, 1141–1146.
Ding, J., & Sperling, G. (2007). Binocular combination: Measurements and a model. In L. Harris & M. Jenkin (Eds.), *Computational vision in neural and machine systems* (pp. 257–305). Cambridge, UK: Cambridge University Press.
Erkelens, C. J. (2000). Perceived direction during monocular viewing is based on signals of the viewing eye only. *Vision Research, 20*, 2411–2419.
Erkelens, C. J., & van De Grind, W. A. (1994). Binocular visual direction. *Vision Research, 34*, 2963–2969.
Erkelens, C. J., & van Ee, R. (2002). The role of the cyclopean eye in vision: Sometimes inappropriate, always irrelevant. *Vision Research, 42*, 1157–1163.
Francis, J. L. & Harwood, K. A. (1951). The variation of the projection center with differential stimulus and its relation to ocular dominance. In *Transactions of the international congress* (pp. 75–87). London British Optical Association.
French, J. W. (1920). The unaided eye, Part III. *Transactions of Optical Society, 21*, 127–156.
Gauthier, G. M., Berard, P. V., Deransard, J. L., Semmlow, J. L., & Vercher, J. (1985). Adaptation processes resulting from surgical correction of strabismus. In E. L. Keller & D. S. Zee (Eds.), *Adaptive processes in visual and oculomotor systems* (pp. 185–189). New York: Pergamon Press.
Gauthier, G. M., Nommay, D., & Vercher, J. (1990). Ocular muscle proprioception and visual localization of targets in man. *Brain, 113*, 1857–1871.
Hariharan-Vilupuru, S., & Bedell, H. E. (2009). The perceived visual direction of monocular objects in random-dot stereograms is influenced by perceived depth and allelotropia. *Vision Research, 49*, 190–201.
Heinrich, S. P., Kromeier, M., Bach, M., & Kommerell, G. (2005). Vernier acuity for stereodisparate objects and ocular prevalence. *Vision Research, 45*, 1321–1328.
Hering, E. (1868/1977). On the bifixation of the double eye. In Bridgeman, B., Stark, L. (Eds.), *The theory of binocular vision* (pp. 17–22). New York: Plenum Press.
Howard, I. P. (1982). Visual direction with respect to the head and body. In *Human visual orientation* (pp. 275–340). New York: John Wiley & Sons.
Krishnan, V. V., Farazian, F., & Stark, L. (1973). An analysis of latencies and prediction in the fusional vergence system. *American Journal of Optometry & Archives of American Academy of Optometry, 50*, 933–939.
Kumar, A. N., Han, Y., Garbutt, S., & Leigh, R. J. (2002). Properties of anticipatory vergence responses. *Investigative Ophthalmology & Visual Science, 43*, 2626–2632.
Li, J., Lam, C. S. Y., Yu, M., Hess, R. F., Chan, L. Y. L., Maehara, G., et al. (2010). Quantifying sensory eye dominance in the normal visual system: a new technique and insights into variation across traditional tests. *Investigative Ophthalmology and Visual Science, 51*, 6875–6881.
Mann, V. A., Hein, A., & Diamond, R. (1979). Localization of targets by strabismic subjects: contrasting patterns in constant and alternating suppressors. *Perception & Psychophysics, 25*, 29–34.
Mansfield, J. S., & Legge, G. E. (1996). The binocular computation of visual direction. *Vision Research, 36*, 27–41.
Mather, J. H. (1969/1983). Visual direction and parameters of binocular space. Thesis (Ph.D.) Bryn Mawr College.
Matin, L., Pearce, D., Matin, E., & Kibler, G. (1966). Visual perception of direction in the dark. Roles of local sign, eye movements, and ocular proprioception. *Vision Research, 6*, 453–469.
McKee, S. P., & Levi, D. M. (1987). Dichoptic hyperacuity: The precision of Nonius alignment. *Journal of the Optical Society of America A, 4*, 1104–1108.
Nakamizo, S., Shimono, K., Kondo, M., & Ono, H. (1994). Visual directions of two stimuli in Panum's limiting case. *Perception, 23*, 1037–1048.
Ogle, K. N. (1972). The theory of corresponding retinal points. In *Researches in binocular vision* (pp. 10–17). Hafner, New York.
Ono, H. (1991). Binocular visual direction of an object when seen as single or double. In *Vision and visual dysfunction*. In D. Regan (Ed.). *Binocular vision* (Vol. 9, pp. 1–18). London: Macmillan.
Ono, H., & Mapp, A. P. (1995). A restatement and modification of Well-Hering's laws of visual direction. *Perception, 24*, 237–252.
Ono, H., Mapp, A. P., & Howard, I. P. (2002). The cyclopean eye in vision: The new and old data continue to hit you right between the eyes. *Vision Research, 42*, 1307–1324.
Ono, H., & Weber, E. U. (1981). Nonveridical visual direction produced by monocular viewing. *Journal of Experimental Psychology: Human Perception & Performance, 7*, 937–947.
Park, K., & Shebilske, W. L. (1991). Phoria, Hering's laws, and monocular perception of direction. *Journal of Experimental Psychology: Human Perception & Performance, 17*, 219–231.
Pointer, J. S. (2007). The absence of lateral congruency between sighting dominance and the eye with better visual acuity. *Ophthalmic and Physiological Optics, 27*, 106–110.
Porac, C., & Coren, S. (1976). The dominant eye. *Psychological Bulletin, 83*, 880–897.
Porac, C., & Coren, S. (1986). Sighting dominance and egocentric localization. *Vision Research, 26*, 1709–1713.
Rashbass, C., & Westheimer, G. (1961). Disjunctive eye movements. *Journal of Physiology, 159*, 339–360.
Rice, M. L., Leske, D. A., Smestad, C. E., & Holmes, J. M. (2008). Results of ocular dominance testing depend on assessment method. *Journal of American Association for Pediatric Ophthalmology & Strabismus, 12*, 365–369.
Robboy, M. W., Cox, I. G., & Erickson, P. (1990). Effects of sighting and sensory dominance on monovision high and low contrast visual acuity. *The Contact Lens Association of Ophthalmologists Journal, 16*, 299–301.
Schor, C. M., Landsman, L., & Erickson, P. (1987). Ocular dominance and the interocular suppression of blur in monovision. *American Journal of Optometry & Physiological Optics, 64*, 723–730.
Schor, C. M., & Tyler, C. W. (1981). Spatio-temporal properties of Panum's fusional area. *Vision Research, 21*, 683–692.
Sheedy, J. E., & Fry, G. A. (1979). The perceived direction of the binocular image. *Vision Research, 19*, 201–211.
Simpson, T. L. (1992). The vergence components and observer-relative direction. Thesis (Ph.D.), University of Houston.
Smith, G., Jacobs, R. J., & Chan, D. C. (1989). Effect of defocus on visual acuity as measured by source and observer methods. *Optometry and Vision Science, 66*, 430–435.
Steinbach, M., & Smith, R. (1981). Spatial localization after strabismus surgery: Evidence for inflow. *Science, 213*, 1407–1409.
Suttle, C., Alexander, J., Liu, M., Ng, S., Poon, J., & Tran, T. (2009). Sensory ocular dominance based on resolution acuity, contrast sensitivity, and alignment sensitivity. *Clinical and Experimental Optometry, 92*, 2–8.
Tadokoro, Y. (1991). Pointing response in normal subjects. *Nippon Ganka Gakkai Zasshi, 95*, 1252–1260.
Toet, A., & Koenderink, J. (1988). Differential spatial displacement discrimination thresholds for Gabor patches. *Vision Research, 28*, 133–143.
Verhoeff, F. H. (1925). A Theory of binocular perspective. *American Journal of Physiological Optics, 6*, 416–448.
Verhoeff, F. H. (1933). Effect of stereopsis produced by disparate retinal images of different luminosities. *Archives of Ophthalmology, 10*, 640–645.
von Holst, E., & Mittelstaedt, H. (1950). Das Reaffernzprinzip. *Naturwissenschaften, 37*, 464–476.
Walls, G. L. (1951). A theory of ocular dominance. *American Medical Association Archives of Opthalmology, 45*, 387–412.
Walls, G. L. (1962). The evolutionary history of eye movements. *Vision Research, 2*, 69–80.
Wheatstone, C. (1838). Contributions to the physiology of vision-part the first. On some remarkable, and hitherto unobserved, phenomena of binocular vision. *Philosophical Transactions of the Royal Society, 128*, 371–394.
Whitaker, D., Bradley, A., Barrett, B. T., & McGraw, P. V. (2002). Isolation of stimulus characteristics contributing to Weber's law for position. *Vision Research, 42*, 1137–1148.
Yang, J., & Stevenson, S. B. (1997). Effects of spatial frequency, duration, and contrast on discriminating motion directions. *Journal of the Optical Society of America A, 14*, 2041–2048.
Yuan, W., Semmlow, J. L., & Munoz, P. (2000). Effects of prediction on timing and dynamics of vergence eye movements. *Ophthalmic & Physiological Optics, 20*, 298–305.